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Antique Forests and Epiphytic Macrolichens in the Kispiox Valley

Background

Lichenologists now generally accept that some lichen species are associated predominantly with late successional or oldgrowth forests. Though few physiological data are available to account for this phenomenon, oldgrowth dependency is assumed to be a function of various attributes (or combinations of attributes) peculiar to oldgrowth ecosystems. For example, humid microclimatic conditions, availability of bark and wood in various stages of soundness and decay, relative environmental stability/continuity, irregular multilayered canopies, and horizontal and vertical patchiness are much greater or better developed in old stands than in young stands.

If it is true that some assemblages of lichens really are oldgrowth-dependent, then it must also be true that an abundance of such lichens indicates advanced forest age. In fact, lichens are routinely used as indicators of relative forest age in other parts of the world. The pioneering work in this field was performed by Francis Rose (1976), who observed that lichen diversity in British forests tends to increase with increasing forest age. No rigorous attempt has been made to apply Rose's observation to the forests of western North America; but here, too, epiphytic lichens could provide important insights into duration of environmental continuity within our oldest forest ecosystems.

In this note, we summarize three years of field work on the epiphytic (= tree-dwelling) macrolichens of the Moist Cold subzone (Hazelton variant) of the Interior Cedar - Hemlock Zone (ICHmc2: Banner et al. 1993). More specifically, our studies were mostly confined to the southern Kispiox Valley where, in our early work, we focussed on lichen floristics and distributional ecology. Later, however, we attempted to use lichens in assessing environmental continuity within selected stands. This note is based on Goward (1992), Goward & Miège (1996), and Goward & Burgess (1996). A more detailed report on this work is in preparation.

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What Are Lichens?

The vast majority of lichens can be classified as Ascomycetes, or cup fungi. This is the same group of fungi to which morels and elf saddles belong. But whereas most cup fungi derive their nourishment from decaying leaves, logs, or other external sources, lichen fungi "cultivate" their foodstuff among the fungal threads of which they themselves are composed. This foodstuff consists of tiny, photosynthetic cells of algae and/or cyanobacteria (formerly called blue-green algae). Lichens can therefore be thought of as living fungal greenhouses supported by carbohydrates derived from the photosynthetic "crops" growing within them. This accounts for the exposed lifestyle typical of lichens: whereas a majority of other fungi live (except when fruiting) hidden inside the things they feed on, lichens colonize the surfaces of things, whether soil, rock or trees. Lichens that colonize trees are referred to as "epiphytic".

The Importance Of Lichens

Lichens are a conspicuous component of many British Columbia ecosystems, and often play an important role in the maintenance of ecosystem health. In many grassland communities, for example, lichen crusts help to protect the soil not only against erosion, but also against encroachment by annual and biennial weeds. In humid forests, lichens can provide an important source of nitrogen. Lichens are also a major source of sustenance for mountain caribou, blacktailed deer and flying squirrels, among other mammals. Many birds, moreover, use lichens as nesting material, whereas numerous nematodes, insects, molluscs and mites rely upon lichens for habitat and, in some cases, food.

Lichens are hardly less useful to humankind. Earlier uses have often been superceded by modern technology, but are nevertheless worth mentoning here. For the native peoples of inland British Columbia, hair lichens once provided the basis for a "vegetable pemmican" that could be stored for use in times of famine. Other species supplied a source of colourful dyes, while still others were woven into makeshift footwear and clothing. Further early applications, especially in Europe, included use as medicines, perfumes and even alcohol. The perfume industry in Europe still relies to some extent on lichens collected from rocky Mediterranean shores.

Contrary to these earlier uses, which were often familiar to the layman, nowadays lichens are used primarily by scientists. In many parts of the industrialized world, pollution-sensitive lichens are used to monitor changes in air quality. Other species concentrate heavy metals and radioactive fallout, and thus provide a convenient measure of environmental contamination, especially as a result of mining. In arctic and alpine localities, geologists are able to estimate the ages of certain rock-dwelling lichens as a means of dating the retreat of glaciers. Back in the laboratory, numerous metabolic substances produced by lichens have been shown to have powerful antibacterial, antiviral and antitumor properties; research in this field is on-going, and new medical applications are being discovered almost yearly.

Epiphytic Lichens Of The Kispiox Valley

The inland oldgrowth "rainforests" of the Kispiox Valley support a rich and highly distinctive epiphytic macrolichen flora. To what extent comparable lichen assemblages occur in other valleys of the Prince Rupert Forest Region is unclear, although the ICHmc2 in the Nass-Kwinageese area appears to have a somewhat similar lichen flora. Even so, the Kispiox Valley is unquestionably an important "epicentre" for lichens. It doubtless owes this distinction to the transitional nature of its climate: the oceanic climate to the west of the Kispiox ICH often favours epiphytic bryophytes (mosses and liverworts) over epiphytic lichens, while the more continental conditions farther inland tend to exclude various "oceanic" species.

A total of 70 macrolichen species has been recorded as epiphytes in the Kispiox Valley, excluding *Cladonia*, which is only facultatively epiphytic, but including *Peltigera*, in which an epiphytic ecology often appears to be associated with advanced forest age. The recorded flora is based on 61 plot studies, many of which were conducted in lichen-rich ecosystems; we assume the list presented in Appendix 1 is reasonably complete, at least for oldgrowth forests.

The Kispiox lichen flora has at least three noteworthy characteristics:

1) the existence of a remarkably diverse cyanolichen component. Cyanolichens are lichens in which the photosynthetic partner consists at least in part of a prokaryotic cyanobacterium (in which the cells lack a discrete nucleus), rather than exclusively of a eukaryotic alga (cells with a discrete nucleus), as in the vast majority of lichens. In the Kispiox Valley, cyanolichens account for nearly half of total epiphytic macrolichen diversity—an incidence hardly equalled in any other region of North America.

2) The Kispiox lichen flora also includes several species which, though elsewhere restricted to oldgrowth forests and other specialized habitats, are here distinctly widespread. Obvious examples include *Cavernularia hultenii, Fuscopannaria ahlneri, Hypogymnia oceanica, H. vittata, Lobaria retigera, Nephroma occultum, Polychidium dendriscum, Sticta fuliginosa* and *S. oroborealis*. The blue-green photomorphs of *Peltigera aphthosa* and *Nephroma arcticum*, as well as the green photomorph of *Sticta oroborealis* also belong here. From this perspective, the Kispiox Valley can be viewed as a critical reservoir of lichen diversity in inland British Columbia.

3) Finally, the Kispiox Valley is also striking for the number of lichen species that do **not** occur here, but that are common in other portions of the ICH. For example, only six epiphytic species of the following genera are known from the Kispiox Valley: *Collema, Evernia, Leptogium, Melanelia, Phaeophyscia, Physcia, Physconia, Ramalina, Usnea* and *Xanthoria*. By contrast, Goward & Ahti (1992) report 38 such species from the ICH of Wells Gray Park and its vicinity.

Epiphytic Lichens And The Toe Position

Epiphytic lichens are not equally diverse in all parts of a forested landscape. In the Kispiox Valley, rare, "oceanic" epiphytes tend to be most diverse in the "toe position", i.e., the basal portions of hillslopes. Toe position ecosystems are generally moister than those in other topopositions, and thus less susceptible to wildfire. Hence the observation that the oldest forest stands in the ICHmc generally occur at the base of hillslopes. By contrast, hillsides, lake shores, narrow ravines, flat valley bottoms, and upland sites are all relatively poor in epiphytic lichens. From these observations, we conclude that inventories conducted in toe-position forests are likely to yield a more or less complete listing of oceanic lichens. Toe-position forests thus provide an appropriate "standard" from which to assess epiphytic macrolichen diversity in old forests.

Epiphytic Lichens And Oldgrowth Dependency

As mentioned earlier, lichen diversity in Britain tends to increase with increasing forest age. In the Kispiox Valley, by contrast, forest age seems to have little effect on species richness among epiphytic macrolichens. Seral forests 40 years old, for example, support roughly the same number of lichens— 41 to 45 species—as do forests 300 years older.

We stress, however, that seral forests and oldgrowth forests support quite different **assemblages** of epiphytic lichens. In fact, 40 year-old forests and 300+ year-old forests display a species overlap of only about 66%, with 18 of 53 species essentially restricted to one age class or the other. Moreover, many additional species are much more common in one or another of the age classes. See Figure 3 for a depiction of these observations, which underline the importance of maintaining forests in all age classes, including very old stands.

More than 20 epiphytic macrolichens are restricted in the study area primarily to oldgrowth

forests (see Appendix 1). All of these species exhibit a requirement for highly "oceanic" conditions, in which humidity remains high, and temperature fluctuations are moderate. Most such lichens would certainly not occur in inland British Columbia in the absence of oldgrowth.

Epiphytic Lichens And The Leachate Effect

As a group, epiphytic cyanolichens are able to establish only over slightly acid to somewhat base-rich substrates (pH above about 5.0). Conifer forests tend to provide more acidic substrates. The presence of cyanolichens in the canopies of such forests probably indicates enrichment, especially by calcium. There is increasing evidence that elevated concentrations of calcium in tree bark are positively correlated with high calcium content in the soil. Presumably calcium is taken up through the roots, and eventually released into the canopy via the leaves and branches.

In the ICHmc, conifers growing within the drip zone of black cottonwood (*Populus balsamifera* subsp. *trichocarpa*) tend to support a rich epiphytic cyanolichen flora. Indeed, such conifers routinely support several cyanolichens not present over other conifers outside the drip zone: *Collema furfuraceum, Leptogium burnetiae, Lobaria hallii, L. pulmonaria, Nephroma resupinatum* and *Peltigera collina*. Other species apparently primarily associated with this enriched habitat include *Collema nigrescens, Lobaria scrobiculata,* and possibly *Nephroma isidiosum, N. parile, Polychidium dendriscum, Sticta fuliginosa* and *S. oroborealis.*

Our observations thus suggest that the colonization of conifers by cyanolichens is strongly enhanced by nutrient enrichment by *Populus*. The phenomenon of above-ground nutrient transfer from one tree genus (*Populus*) to another (*Abies, Tsuga*, etc.) may be described as a "leachate effect". Based on studies in other parts of the ICH (Goward & Arsenault, in prep.), the leachate effect appears to represent the downward migration of nutrients as a result of rain splash and canopy snowmelt.

Nitrogen is usually the key element in short supply in humid coniferous forests. Cyanolichens are able to "fix" atmospheric nitrogen, which they thus make available to the environments in which they occur. Black cottonwood and indeed other members of the Salicaceae (willow family) can be considered catalysts for the introduction of nitrogen into regenerating ICH forests. We do not know to what extent epiphytic cyanolichens contribute to the nitrogen budget in these Kispiox ecosystems, but researchers in the Pacific Northwest estimate that *Lobaria oregana* fixes 3 kg/ha/y (which some assert represents about 50% of total nitrogen input) in oldgrowth Douglas-fir forests (Rhoades 1995). For this and other reasons, we do not think that attempts to control cottonwood and willows in young plantation forests make ecological sense.

Assessing For Forest Antiquity: Lichenological Indicators

Many of British Columbia's oldgrowth forests have originated as a result of fire, and are probably no older than the oldest trees within them. By contrast, environmental continuity in other oldgrowth forests may considerably pre-date the oldest trees. Goward (1994) has termed multigenerational forests of this kind "antique".

Fire-formed forests in early and middle succession may be reliably aged using core sample techniques. No simple method, however, is currently available to age antique forests. Because environmental continuity in such forests extends beyond the age of the oldest trees, duration of environmental continuity is here much more difficult to assess. Radiocarbon dating of charcoal fragments holds some promise, but those who adopt this technique must distinguish between localized lightning strikes and actual stand-replacing wildfires. In the present study, we initially attempted to identify antique forests on the basis of epiphytic "indicator" lichens alone. Because, however, at least some of these lichens are favoured equally by forest age and by the leachate effect, we found it necessary to amplify our assessments using a variety of unrelated indicators of continuity. One especially critical benchmark of forest continuity in the ICHmc is *Lobaria oregana* (Fig. 1). This species appears to disperse primarily via fragmentation of coarse marginal

lobules (preformed fragments): a rather inefficient mechanism of dispersal, to judge from its obvious slow rates of colonization. Even once *L. oregana* does become established at a site, it appears to require many decades, or more probably centuries, to become widespread and abundant within it. Based on this observation, we assume that forests in which this species occurs in abundance are very old— at least in the Kispiox Valley.

We also assume that the greater the number of "oceanic" lichens present in a given forest stand, the older the stand. The following species appeared to be useful indicators of stand age: *Cavernularia hultenii, Fuscopannaria ahlneri, F. mediterranea, Hypogymnia apinnata, H. enteromorpha, H. oceanica, H. rugosa, H. vittata, Lichinodium canadense, Lobaria linita, L. oregana, L. retigera, L. silvae-veteris, Nephroma isidiosum, N. occultum, Platismatia norvegica, Polychidium dendriscum, Sphaerophorus globosus, S. tuckermanii, Sticta fuliginosa, S. oroborealis* and *S. wrightii*. In general, we considered as candidates for antique status all forests stands supporting nine or more of these lichens. Even so, a few stands supporting 11 or more indicator species were rated as "possibly antique" or "not antique", based on the absence or poor development of various other (i.e., nonlichenological) criteria of extreme old age.

FIGURE 1. ***Lobaria oregana*** **(lettuce lung). Photo by A. Roberts**

Assessing For Forest Antiquity: Other Indicators

We amplified our lichenological assessments of forest antiquity using several additional presumed indicators of forest age. Among these are: micromounding; large logs in an advanced state of decomposition; and evidence of the presence of large old black cottonwood trees earlier in the life of the stand.

1) **Micromounding.** As old trees die and topple, their roots often become upturned, thereby creating sizable tip-up mounds or root-wads. Observations in the Kispiox Valley and elsewhere suggest that such mounds tend to increase in number with increasing forest age, though of course older, well decayed mounds are detectable merely as low bumps. We therefore assume that the occurrence of abundant and variable micromounding is a reliable indicator of considerable forest age. Younger oldgrowth forests often lack conspicuous micromounding.

2) **Well Decayed Large Logs.** Very old oldgrowth forests usually contain large downed logs in a wide range of decay classes. By contrast, younger oldgrowth forests characteristically have large logs in only a moderate state of decay. In using logs as indicators of relative forest age, however, it is important to check for evidence of fire scars.

3) **Black Cottonwood.** After fire, disturbed sites in many portions of the ICH are often colonized by black cottonwood. In most topopositions, however, this species is eventually excluded by increasing shade from the regenerating conifer canopy. Only in the toe position, where canopy structure tends to be open, does black cottonwood regularly persist into late succession. Even here, however, it eventually succumbs to decay, and is typically replaced by conifers. The absence of black cottonwood in humid toe position oldgrowth forests could thus be taken as a qualified indicator of great age. In some antique forests, one can surmise the former presence of this species by the occurrence of localized heavy loadings of *Antitrichia curtipendula* and other bryophytes on the branches of conifers; such loadings often result from nutrient enrichment by black cottonwood.

Antique Forests Of The Kispiox Valley

In total, we assessed 37 oldgrowth stands in the Kispiox Valley for antique status (Fig. 2). Based on the indicators discussed in the previous sections, 13 of these were judged to be antique, while another 14 did not exhibit signs of advanced age. Ten stands appeared to be intermediate between these two extremes. All 37 stands have been located on forest cover maps. The oldest stands have also been delineated on aerial photographs located at the Kispiox District office of the Ministry of Forests.

Conclusions

Figure 3 on page 8 summarizes our interpretation of the developmental stages in toe-position ICHmc forests of the Kispiox Valley, and the associated changes in epiphytic macrolichens. Again we stress that forests of all age classes, including very old, are important for maintaining the diversity of epiphytic lichens.

Modern forestry adversely affects epiphytic lichen diversity in several ways: 1) by causing a decline in various structural components typical of old forests; 2) by altering microclimatic conditions beyond the tolerance of many species; 3) by interrupting ecological continuity at relatively frequent intervals; and 4) by causing a decline in the extent of and connectivity among oldgrowth patches.

Until recently, the lower Kispiox Valley supported extensive stands of antique, oldgrowth and/or late successional conifer forests. Though natural disturbances—fire, insect outbreak, windthrow—have presumably driven stand dynamics for thousands of years, the resulting forest mosaic has doubtless always incorporated old forests. Only very recently have oldgrowth forests essentially disappeared from the lower portions of the valley. In future, every effort should be made to ensure that cutting practices do not jeopardize the oldest remaining oldgrowth ecosystems which, according to our studies, support the richest macrolichen assemblages. Wholesale plantation forestry will probably doom many epiphytic lichens in this critical portion of British Columbia.

Given the ability of cyanolichens to fix atmospheric nitrogen, and hence to contribute nitrogen to the ecosystems in which they occur, significant reduction in these species will reduce ecosystem integrity, and could adversely affect forest productivity.

Epilogue

The antique "rainforests" of the Kispiox Valley support one of the world's richest epiphytic cyanolichen floras—in many ways comparable to the cyanolichen floras of temperate New Zealand, Tasmania, and Chile. Here many species display a much broader ecological amplitude than in other portions of their range; and a few develop forms otherwise unknown in North America. The importance of the Kispiox Valley in the maintenance of cyanolichen diversity in inland British Columbia can hardly be overstated.

Of course, antique forests are worthy of conservation efforts in their own right. Such forests have probably never been very abundant in lowland British Columbia, except in some coastal regions. Their typical association with topographically gentle sites makes them highly vulnerable to logging, road construction and, in some regions, flooding by hydro-electric dams.

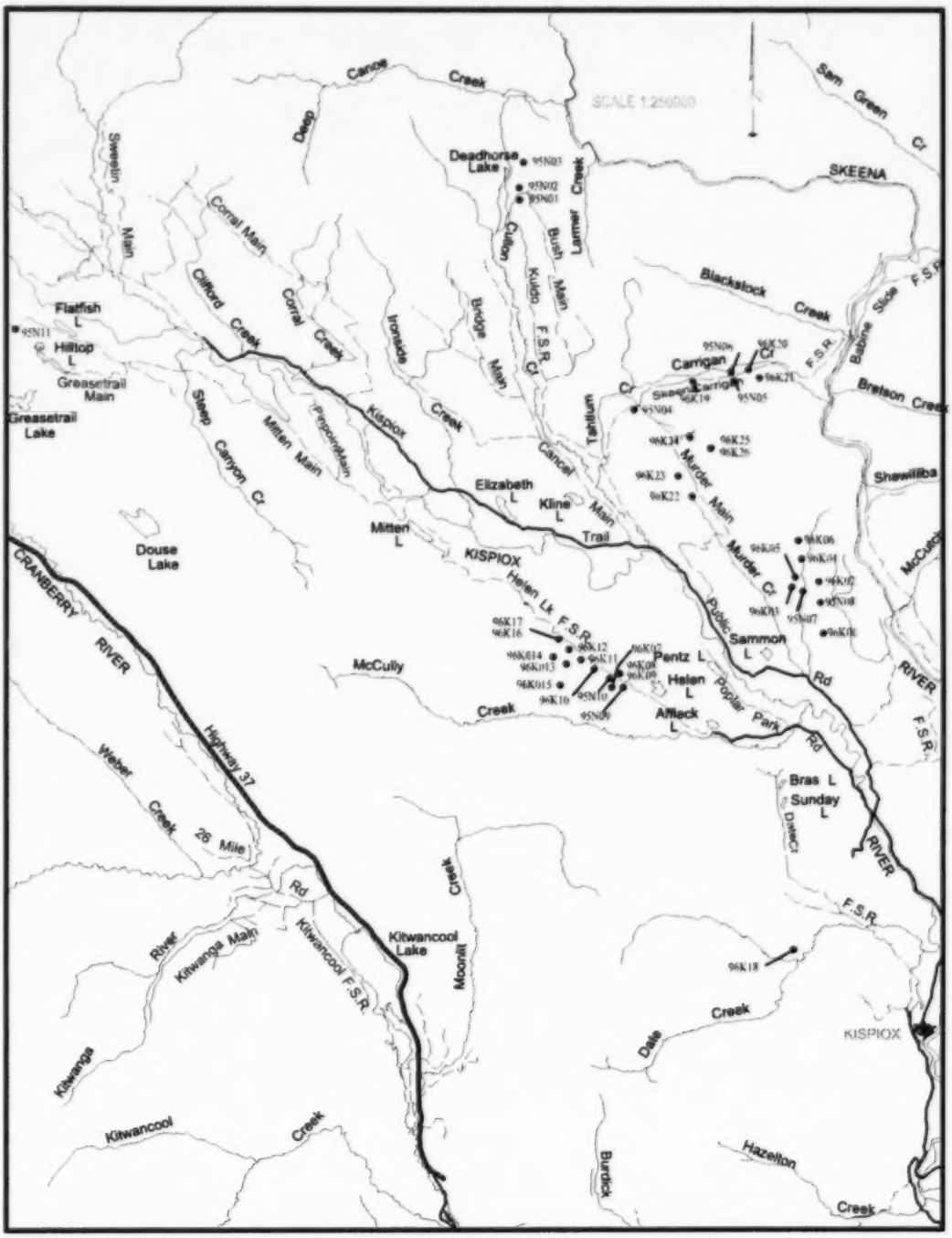

FIGURE 2. Location of 37 plots in oldgrowth ICHmc forests of the Kispiox Valley

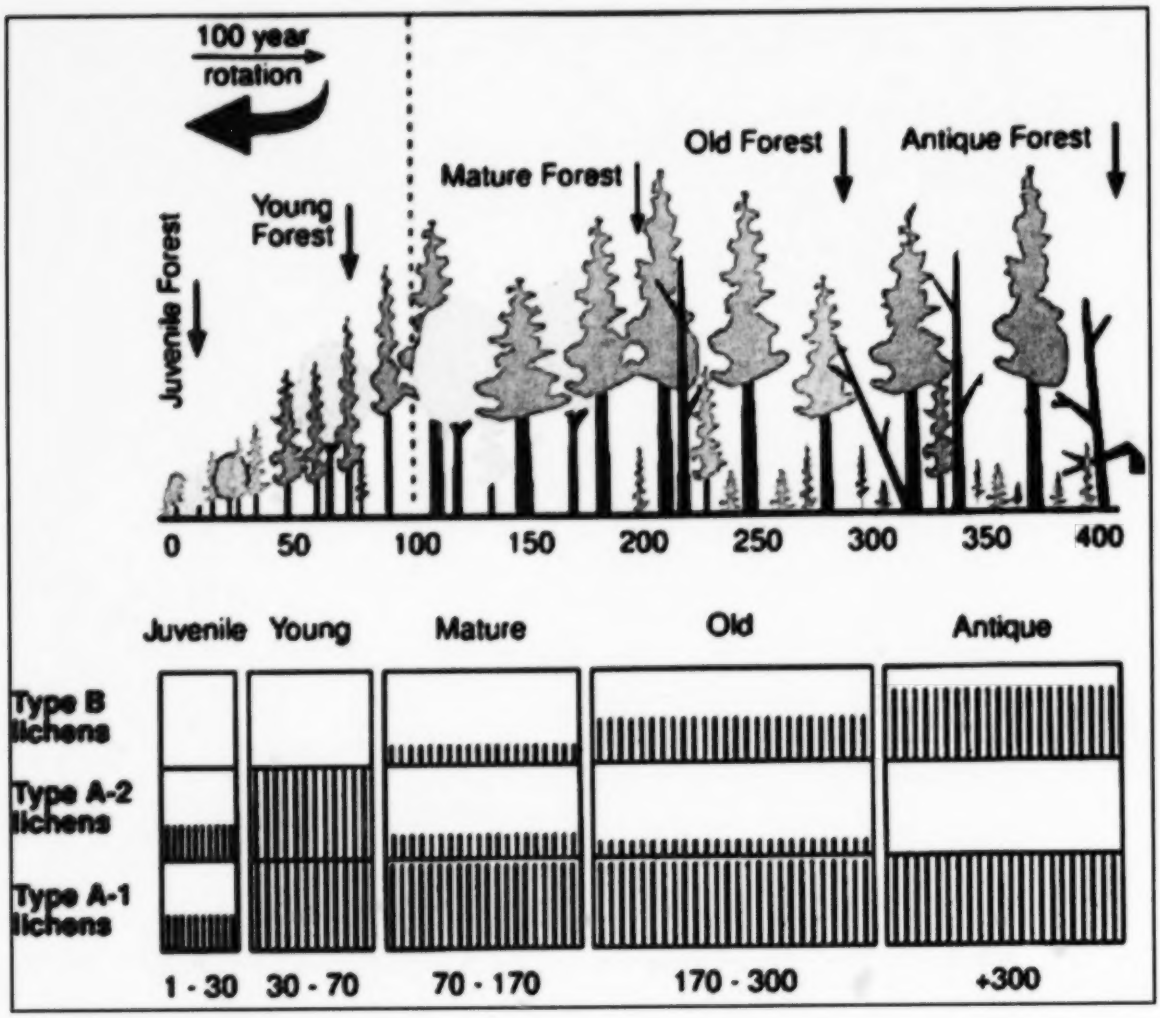

FIGURE 3. Stand age, development stage, and epiphytic macrolichens in toe-position ICHmc forests of the Kispiox Valley. Type A-1 (terminology of Goward 1994, 1995) lichens are widespread generalists that occur in forests of all age classes and developmental stages. Type A-2 lichens are also widespread species but are restricted primarily to younger forests. Type B lichens are specialists restricted primarily to oldgrowth forests.

Not surprisingly, antique forests are currently among the most endangered of the province's ecosystems. If only as archives of British Columbia's biological past, they deserve special consideration as candidates for protected status.

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Appendix 1. Epiphytic Macrolichens Of The Kispiox Valley

Note: The species appearing in bold are associated (as epiphytes) with oldgrowth forests in the study area.

Ahtiana pallidula (Riddle) Goward & Thell
(pallid ruffle)
Alectoria sarmentosa (Ach.) Ach.
(common witch's hair)
Bryoria fremontii (Tuck.) Brodo & D. Hawksw.
(edible horsehair)
Bryoria fuscescens (Gyelnik) Brodo & D. Hawksw.
(speckled horsehair)
Bryoria trichodes (Michaux) Brodo & D. Hawksw. ssp. *americana* (Mot.) Brodo & D. Hawksw.
(bay horsehair)
Cavernularia hultenii Degel.
(powdered honeycomb)
**Collema furfuraceum* (Arnold) Du Rietz
(blistered tarpaper)
**Collema nigrescens* (Hudson) DC.
(broadleaf tarpaper)
Fuscopannaria ahlneri (P.M. Jørg.) P.M. Jørg.
(roughened mouse)
Fuscopannaria mediterranea (Tavares) P.M. Jørg.
(blue-eared mouse)
Hypogymnia apinnata Goward & McCune
(beaded pipe/bone)
Hypogymnia enteromorpha (Ach.) Nyl.
(beaded pipe/bone)
Hypogymnia imshaugii Krog
(forked pipe/bone)
Hypogymnia inactiva (Krog) Ohlsson
(forked pipe/bone)
Hypogymnia metaphysodes (Asah.) Rass.
(deflated pipe/bone)
Hypogymnia occidentalis Pike
(lattice pipe/bone)
Hypogymnia oceanica Goward
(powdered lattice pipe/bone)
Hypogymnia physodes (L.) Nyl.
(grey monk's hood)
Hypogymnia rugosa (G.K. Merr.) Pike in Hale
(puckered pipe/bone)
Hypogymnia tubulosa (Schaerer) Havaas
(dog pipe/bone)
Hypogymnia vittata (Ach.) Parr
(brown monk's hood)
Imshaugia aleurites (Ach.) S.F. Meyer
(salted starburst)
Kaernefeltia merrillii (Du Rietz) Thell & Goward
(olive thornbush)
**Leptogium burnetiae* Dodge
(peppered vinyl)
Lichinodium canadense Henssen
(oldgrowth woollybear)
**Lobaria hallii* (Tuck.) Zahlbr.
(iron lung)
****Lobaria linita*** (Ach.) Rabenh.
(cabbage lung)
****Lobaria oregana*** (Tuck.) Müll. Arg.
(lettuce lung)
**Lobaria pulmonaria* (L.) Hoffm.
(lungwort)
****Lobaria retigera*** (Bory) Trevisan
(smoker's lung)
**Lobaria scrobiculata* (Scop.) DC.
(textured lung)
****Lobaria silvae-veteris*** (Goward & Goffinet) Goward & Goffinet
(oldgrowth lung)
****Nephroma arcticum*** (L.) Torss.
(greenlight/green paw)
**Nephroma bellum* (Sprengel) Tuck.
(cat's paw)
**Nephroma helveticum* Ach. ssp. *sipeanum* (Gyelnik) Goward & Ahti
(dog's paw)
****Nephroma isidiosum*** (Nyl.) Gyelnik
(peppered paw)
****Nephroma occultum*** Wetm.
(cryptic paw)
**Nephroma parile* (Ach.) Ach.
(powdered paw)

Appendix 1 continued

**Nephroma resupinatum* (L.) Ach.
(blistered paw)
Parmelia hygrophila Goward & Ahti
(salted shield)
Parmelia pseudosulcata Gyelnik
(salted shield)
Parmelia saxatilis (L.) Ach.
(salted shield)
Parmelia sulcata Taylor
(waxpaper/powdered shield)
Parmeliopsis ambigua (Wulfen) Nyl.
(green starburst)
Parmeliopsis hyperopta (Ach.) Arnold
(grey starburst)
****Peltigera aphthosa*** (L.) Willd.
(freckle pelt)
****Peltigera britannica*** (Gyelnik) Holtan-Hartw. & Tønsb.
(freckle pelt)
**Peltigera collina* (Ach.) Schrader
(tree pelt)
****Peltigera membranacea*** (Ach.) Nyl.
(dog pelt)
****Peltigera neopolydactyla*** (Gyelnik) Gyelnik
(frog pelt)
****Peltigera pacifica*** Vitik.
(fringed frog pelt)
Platismatia glauca (L.) Culb. & C. Culb.
(ragbag)
Platismatia herrei (Imsh.) Culb. & C. Culb.
(tattered rag)
Platismatia norvegica (Lynge) Culb. & C. Culb.
(laundered rag)
Polychidium contortum Henssen
(woolly woollybear)
Polychidium dendriscum (Nyl.) Henssen
(woolly woollybear)
**Pseudocyphellaria anomala* Brodo & Ahti
(netted specklebelly)
Ramalina dilacerata (Hoffm.) Hoffm.
(punctured gristle)
Ramalina thrausta (Ach.) Nyl.
(angel hair)
Sphaerophorus globosus (Hudson) Vainio
(unkempt coral)
Sphaerophorus tuckermanii Räsänen
(elegant coral)
**Sticta fuliginosa* (Hoffm.) Ach.
(peppered moon)
****Sticta limbata*** (Sm.) Ach.
(powdered moon)
****Sticta oroborealis*** Goward & Tønsberg
(black bonsai/green moon)
****Sticta wrightii*** Tuck.
(green moon)
Tholurna dissimilis (Norman) Norman
(bottle collection)
Tuckermannopsis chlorophylla (Willd.) Vainio
(powdered ruffle/shadow ruffle)
Tuckermannopsis orbata (Nyl.) Hale
(variable ruffle)
Usnea spp.
(beard lichens)
Vulpicida canadensis (Räsänen) J.-E. Mattsson & M.J. Lai
(brown-eyed sunshine)
Vulpicida pinastri (Scop.) J.-E. Mattsson & M.J. Lai
(powdered sunshine)

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*Lichens that contain a cyanobacterial partner.